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Heterosis and combining ability of highland quality protein maize inbred lines

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Abstract

Quality protein maize (QPM) cultivars contain higher levels of lysine and tryptophan as compared to non-QPM counterparts, and can minimize the risk of protein malnutrition among communities increasingly dependent on maize as their food staple. This study was undertaken to assess the performances of QPM hybrids, and estimate heterosis and combining ability effects of highland QPM inbred lines for grain yield, agronomic and protein quality traits. Hybrids of 20 inbred lines and two testers, and the parental lines were evaluated across three locations in Ethiopia. Significant variations were observed among the parents and the hybrids for almost all measured traits that allows the selection of preferred inbred lines and hybrids. Several hybrids showed desirable heterosis for most studied traits. Mean squares attributable to general (GCA) and specific (SCA) combining ability effects were significant for most traits. However, the contributions of GCA sum of squares to the variation among the hybrids were larger than SCA sum of squares, suggesting that the traits were conditioned mainly by additive gene effects. Inbred lines L12, L17, L19, and L20 had desirable GCA effects for grain yield, whereas L12 and L13 were the best general combiners for protein quality traits. Hybrids L17 x 142-1eQ and L20 x 142-1-eQ showed most desirable perse performances and SCA effects for grain yield. Based on grain yield SCA effects, most inbred lines used in the study were grouped into distinctive heterotic patterns. This study indicated the possibility of developing highland QPM germplasm with acceptable grain yield, agronomic and protein quality traits.

Keywords: combining ability, heterosis, heterotic group, quality protein maize

Introduction

Maize is grown over a wider range of environmental conditions than any other food crops. The global area is about 184 million ha with corresponding average annual production of over one billion metric tons (FAOSTAT, 2014). It is larger than the production of the two other major staple cereals, wheat and rice, and serves as major source of calories in human diets in many developing countries (Shiferaw et al, 2011). In Africa, maize covers a total of 35 million ha that accounts for 19% of the total global maize area. Africa's total share of maize production, however, is 72 million metric tons, accounting only for about 7% of world production (FAOSTAT, 2014). In Ethiopia, maize is grown on about 2.0 million ha with annual production of 6.5 million tons (CSA, 2014). It is second to tef (Eragrostis tef) in area coverage but first in productivity and total production among all cereals. In major maize producing areas of the country, it is a staple food while in other regions it is used in mixtures with other food grains.

However, similar to other cereals, maize is known to be of poor protein nutritional quality, due to lysine and tryptophan deficiency (Twumasi-Afriyie et al, 2012). Hence, protein malnutrition is common among children whose diet is dominated by maize and other cereals. The discovery of the biochemical effects of mutant allele *o2* (Mertz et al, 1964) opened an opportunity for improving the quality of maize endosperm protein. This mutant alters amino acid profile and composition of maize endosperm protein and results in two-fold increase in the levels of lysine and tryptophan compared to what is observed in the non-QPM genotypes (Villegas et al, 1992). However, commercial exploitation of o2 germplasm has been subsided by certain undesirable pleiotropic effects of the *o2* mutation. International Maize and Wheat Improvement Center (CIMMYT) used a backcross-cum-recurrent selection procedure to accumulate the hard endosperm phenotype and developed genotypes with elevated lysine and tryptophan content relative to non-QPM (Vasal, 2001).

Several African maize breeding programs are using the publicly available CIMMYT's QPM germplasm due to the relatively high costs and difficulties linked to QPM breeding for the development of locally adapted QPM cultivars. In recent years, however, a number of released and popular non-QPM cultivars (open-pollinated varieties and parental inbred lines of hybrids) are converted to QPM versions in Ethiopia (Twumasi-Afriyie et al, 2012). For the conversion, QPM donor stocks suitable for each non-QPM

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germplasm were sourced from CIMMYT maize lines (CMLs).

Information about heterosis and combining ability of experimental breeding materials is imperative to a breeding program aiming to develop high yielding hybrids and composite varieties (Hallauer and Miranda, 1988). Vasal et al (1993) studied heterosis and combining ability of CIMMYT's lowland tropical QPM germplasm and reported the existence of parent heterosis and the greater importance of GCA relative to SCA. Combining ability studies of QPM inbred lines conducted by Pixley and Bjarnason (1993) and Musila et al (2010) indicated the preponderance of GCA or additive gene action for grain yield and agronomic traits. However, Wegary et al (2011; 2014) found both GCA and SCA effects to be significant and important for grain yield. In the study of Machida et al (2010), only SCA effects were significant for grain yield. For the protein quality traits and endosperm modification, almost all the earlier studies cited above indicated the greater importance of GCA effects than that of SCA.

In Ethiopia, the heterotic effects and combining abilities of newly developed highland QPM germplasm have not been studied so far. Hence, it would be interesting to investigate the heterosis and components of genetic variation that are exhibited by this germplasm for future exploitations in the breeding programs. This study was undertaken to: (i) assess the performances of QPM inbred lines and testcrosses for grain yield, agronomic traits and protein quality traits, and (ii) estimate heterosis and combining ability effects for these traits.

Materials and Methods

Germplasm

Twenty newly converted QPM inbred lines were selected and crossed with two testers, 142-1-eQ and F7215Q, using the method described by Singh and Chaudary (1999) at Ambo Research Center during the main season of 2006 that resulted into 40 F_1 progenies. The lines were selected based on vigor, general adaptation and resistance to major diseases of the highland regions. F7215Q and 142-1-eQ were derived from Kitale Synthetic-II and Ecuador 573, respectively, which are well known heterotic populations in Eastern African highland maize ecologies (Darrah, 1986). Four commercial check hybrids, namely, AMH800, BH6660, BH540 and BHQP542 were used in the trials. AMH880 and BH660 are widely adapted non-QPM hybrids released for highland, and mid-altitude to transitional highland ecologies, respectively. BH540 is a very popular medium maturing hybrid released for mid-altitude high potential maize growing ecologies; and in some instances used in transitional highland areas. BHQP542 (CML144/CML159//CML176) is a mid-altitude QPM hybrid that has been released in many African countries including Ethiopia. The pedigree and genetic backgrounds of the inbred lines and the testers used for the study are given in Table 1.

Experimental design and field management

Parental lines and hybrids were evaluated in separate trials planted adjacent to each other at three highland locations; namely, Ambo, Holeta and Kulumsa. Ambo lies at 8°57'N;8°07'E at an altitude of 2,225 masl; Holeta lies at 9°00'N;34°48'E at an altitude of

Table 1 - Pedigrees and sources of quality protein maize inbred lines and testers used for the study.

Designation	Pedigree	Source
Lines		
L1	[POOL9Ac7-SR(BC2)]FS195-2SR-1-2-2-1-#/CML144(BC2)-5-1-2	Pool9A
L2	[POOL9Ac7-SR(BC2)]FS45-3-2-2-1-#/CML144(BC2)-8-14-1	Pool9A
L3	[POOL9Ac7-SR(BC2)]FS67-1-2-3-1-#/CML144(BC2)-10-6-1	Pool9A
L4	[POOL9Ac7-SR(BC2)]FS68-1-1-2-2-#/CML144(BC2)-11-6-1	Pool9A
L5	[POOL9Ac7-SR(BC2)]FS71-1SR-2-1-2-#/CML144(BC2)-16-10-1	Pool9A
L6	[POOL9Ac7-SR(BC2)]FS112-4-2-1-1-2-#/CML144(BC2)-25-12-2	Pool9A
L7	[POOL9Ac7-SR(BC2)]FS112-4-2-1-1-2-#/CML144(BC2)-25-18-4	Pool9A
L8	[KIT/SNSYN[N3/TUX]]c1F1-##(GLS=2)-29-35-2-3/CML144(BC2)-29-5-3	Kitale Synthetic-II
L9	[POOL9Ac7-SR(BC2)]FS67-1-2-2-1/CML144(BC2)-32-13-3	Pool9A
L10	[ECU/SNSYN[SC/ETO]]c1F1-##(GLS=1)-34-3-1-2/CML144(BC2)-34-8-2	Ecuador 573
L11	[ECU/SNSYN[SC/ETO]]c1F1-##(GLS=1)-34-3-1-2/CML144(BC2)-34-13-2	Ecuador 573
L12	[ECU/SNSYN[SC/ETO]]c1F1-##(GLS=3.5)-3-2-1-#/CML176(BC2)-11-5-2	Ecuador 573
L13	[POOL9Ac7-SR(BC2)]FS4-3SR-1-1-1-#/CML176(BC2)-6-1-1	Pool9A
L14	[POOL9Ac7-SR(BC2)]FS59-2-2-1-1-#/CML144(BC2)-9-2-3	Pool9A
L15	[POOL9Ac7-SR(BC2)]FS68-1-1-2-1-1/CML144(BC2)-33-4-1	Pool9A
L16	[POOL9Ac7-SR(BC2)]FS69-1SR-1-2-1-#/CML176(BC2)-1-2-1	Pool9A
L17	[ECU/SNSYN[SC/ETO]]c1F1-##(GLS=3.5)-3-2-1-#/CML176(BC2)-6-2-2	Ecuador 573
L18	[POOL9Ac7-SR(BC2)]FS48-1-1-1-1-1-#/CML144(BC2)-6-25-1	Pool9A
L19	[ECU/SNSYN[SC/ETO]]c1F1-##(GLS=3.5)-3-2-1-#/CML176(BC2)-3-3-1	Ecuador 573
L20	[POOL9Ac7-SR(BC2)]FS68-1-1-2-1-1/CML144 (BC2)-33-1-1	Pool9A
Testers		
T1	142-1-e Q (Line tester)	Ecuador 573
T2	F7215Q (Line tester)	Kitale Synthetic-II

Table 2 - Analysis of variance and means for grain yield, agronomic and protein quality traits of highland quality protein maize parental lines evaluated across three locations in Ethiopia.

Source	DF	GY (t ha^{-1})	TKW (g)	AD (d)	SD (d)	PH (cm)	EH (cm)	EPP (No.)	MODI (1-5)	TRP (g kg^{-1})	PROT (g kg^{-1})	QI (%)
Location (L)	2	154.4**	21308**	9719**	6890**	15736**	5693**	3.36**	0.14	0.02	636.2**	0.02
Replication/L	3	0.73	4194	37.35	26.77	537.0	201.6	0.02	0.71	0.04	41.2	0.02
Parents (P)†	21	2.6**	4434	112.1**	118.7**	3115**	1721**	0.15**	1.37	0.08 **	401.6**	0.06**
P x L	42	1.14 **	3897	34.67	23.08**	281.7	261.0**	0.08**	1.58	0.03	84.4	0.02*
Error	63	0.51	2686	23.5	12.0	206.9	100.6	0.04	1.19	0.02	79.9	0.01
Mean		2.83	252	109	114	170	88.2	1.26	2.43	0.74	113	0.65
Minimum		1.77	202	103	109	130	61.8	0.98	1.50	0.56	98.2	0.49
Maximum		4.04	298	118	123	230	134	1.55	3.33	1.04	131	0.85
SE(m)±		0.29	21.16	1.98	1.41	5.87	4.10	0.08	0.45	0.06	3.65	0.04

†Parents include inbred lines and testers;* P< 0.05, ** P< 0.01, DA = days to anthesis, DF = Degrees of freedom, DS = Days to silking, EH = ear height, EPP = Ears per plant, GY = Grain yield, MODI = Endosperm modification, PH = Plant height, PROT = Protein content, QI = Quality index, TKW = Thousand kernel weight, TRP = Tryptophan content.

2,390 masl; and Kulumsa lies at at 8°13'N;39°13'E at an altitude of 2,200 masl. The soil types of Ambo, Holeta, and Kulumsa are characterized by Vertisols, Nitisols, and Luvisols and the areas receive average annual rainfall of 1,115, 1,065, and 832 mm, respectively. Mean minimum and maximum temperatures are 11.7°C and 25.4°C for Ambo; 6.4°C and 22.1°C for Holeta, and 10.0°C and 23.0°C for Kulumsa, respectively.

The inbred line trial consists of 20 parental inbred lines and two testers, while the hybrid trial consisted of 40 testcrosses and four check hybrids. Experimental designs were alpha (0,1) lattice (Patterson and Williams, 1976) with two replications at each location. The plots consisted of two rows for line trials and a single five-meter long row for the hybrids with 75 cm spacing in between rows and 25 cm between plants. Plots were planted with two seeds per hill and later thinned to one plant per hill resulting in a plant population of about 53,333 plants ha^{-1} at all locations. Nitrogen fertilizer at the rate of 100 kg ha^{-1} was applied in two splits, half at planting and the rest at 37 days after emergence while 100 kg P_2O_5 ha^{-1} was applied at planting. Pre-emergence herbicide, Lasso-Atrazin (5.0 l ha^{-1}), was applied at planting to control weeds; and then the weeds were controlled by hand weeding. All other management practices were performed according to the recommendations for each location.

Field measurements

Field data were recorded for grain yield, agronomic traits and endosperm modification. Grain yield was measured from all the ears of each experimental unit, adjusted to 12.5% moisture content and expressed in ton ha^{-1}. Days to anthesis and silking were recorded as the number of days from planting to 50% pollen shed and silk emergence. Two weeks after pollen shed, plant and ear heights were measured as the distance from ground level to the first tassel branch and upper ear bearing node, respectively. For thousand kernel weight, random kernels from the bulk of each experimental unit after shelling was counted using a photoelectric seed counter and weighed in grams after the moisture was adjusted to 12.5%. Endosperm modification was recorded as an average of all ears of each experimental unit using 1 – 5 rating scale according to Vivek et al (2008). The ratings were interpreted as 1 = not opaque and endosperm wholly translucent; 2 = 25% opaque; 3 = 50% opaque; 4 = 75% opaque and 5 = 100% opaque.

As indicated by Wegary et al (2011), when non-QPM pollinates QPM, the resultant endosperm immediately loses protein quality. In order to sample QPM grain for laboratory analysis, 2-3 plants in each plot were sib-mated (plant-to-plant full sibbing). The sib-mated plants in each plot were harvested and shelled separately for laboratory analysis while the rest of the plants in the plot were used for estimation of grain yield per hectare as indicate above. F_2 grains were shelled from the middle of the sib-mated cobs. Random sample of 20 seeds of uniform size were taken from the bulk grains of each plot for laboratory analysis of protein and tryptophan content.

Laboratory methods

Protein content and quality were determined at the CIMMYT Cereal Quality Laboratory following procedures described by Villegas et al (1984). Briefly, whole-grain samples were finely ground using 0.5 mm setting of a cyclone mill, the resulting flour was defatted with hexane, and concentrations of nitrogen and tryptophan were colorimetrically determined for duplicate samples. Protein concentration was estimated from the nitrogen value as: % protein = % nitrogen × 6.25 (conversion factor for maize). Tryptophan and protein concentrations in grain were expressed as g kg^{-1} for statistical analysis. Protein quality index was calculated as the ratio of tryptophan concentration to protein concentration in the whole grain sample, expressed as a percentage. Lysine concentration was not measured because the procedure is more costly and lengthy than tryptophan analysis, and because lysine and tryptophan concentrations in the protein of o2 endosperm are highly correlated, r = 0.85; P < 0.01 (Hernandez and Bates, 1969). The use of whole grain for colorimetric determination of protein quantity and quality has been used effectively to improve QPM germplasm at CIMMYT and seems justifiable in light of the considerable cost savings realized (Pixley and Bjarnason, 1993).

Table 3 - Mean grain yield, agronomic and protein quality traits of the QPM lines and testers evaluated across three locations in Ethiopia.

Designation	GY (t ha^{-1})	TKW (g)	DA (d)	DS (d)	PH (cm)	EH (cm)	EPP (No.)	MODI (1-5)	TRP (g kg^{-1})	PROT (g kg^{-1})	QI (%)
Inbred lines											
L1	2.12	279	107	112	138	72	1.13	2.33	0.58	118	0.49
L2	1.84	237	106	115	130	69	0.98	2.67	0.91	122	0.75
L3	2.62	258	110	112	179	96	1.00	1.83	0.79	118	0.67
L4	2.48	298	107	110	157	85	1.50	2.50	0.83	115	0.71
L5	2.99	222	110	113	139	63	1.40	2.33	0.74	122	0.61
L6	2.91	229	106	109	188	75	1.38	2.50	0.70	105	0.66
L7	3.24	258	108	110	169	88	1.22	3.00	0.56	114	0.49
L8	3.56	267	106	111	156	77	1.55	2.67	-	-	-
L9	3.65	254	107	112	169	80	1.52	2.00	0.61	98	0.62
L10	4.04	246	110	113	174	84	1.27	2.33	0.79	118	0.67
L11	2.74	223	104	109	181	87	1.22	1.67	0.66	103	0.63
L12	2.28	202	117	119	188	99	1.20	2.17	0.77	131	0.59
L13	2.26	232	103	109	138	62	1.27	2.83	1.07	123	0.87
L14	2.67	292	108	111	172	92	1.15	3.00	0.74	108	0.69
L15	3.69	267	107	112	187	91	1.25	2.00	0.66	119	0.55
L16	2.86	202	113	121	176	95	1.53	1.50	0.58	118	0.49
L17	3.59	291	109	119	184	104	1.20	3.00	0.88	112	0.78
L18	2.73	256	108	113	147	75	1.18	2.83	0.88	109	0.80
L19	2.57	228	117	123	182	108	1.18	2.83	0.80	114	0.71
L20	1.98	257	118	119	187	100	1.13	3.33	0.78	110	0.71
Testers											
142-1-eQ	3.74	269	117	122	230	134	1.25	2.17	0.71	100	0.71
F-7215Q	1.77	266	111	115	169	106	1.18	2.17	0.60	112	0.54
Mean	2.83	252	109	114	170	88	1.26	2.44	0.74	114	0.65
CV(%)	24.21	20.20	4.37	3.06	10.71	12.69	15.74	45.37	20.29	7.78	17.32
$LSD_{(0.05)}$	0.84	57.9	5.56	4.04	21.39	13.30	0.23	1.24	0.17	10.0	0.13

DA = days to anthesis, DF = degrees of freedom, DS = days to silking, EH = ear height, EPP = Ears per plant, GY = Grain yield, MODI = Endosperm modification, PH = Plant height, PROT = Protein content, QI = Quality index, TKW = Thousand kernel weight, TRP = Tryptophan content.

Statistical analysis

Analysis of variance per environment was conducted using individual plot data with the PROC MIXED procedure in SAS (2004), considering genotypes as fixed effects and replications and incomplete blocks within replications as random. Entry means adjusted for block effects generated from individual location analyses according to the lattice design were used to perform combined analyses across environments using PROC GLM in SAS (2004). Mean squares for hybrids and environments were tested against the mean squares for hybrid x environment as error term whereas hybrid x environment mean squares were tested against pooled error.

Mid-parent heterosis was calculated as:

$$MPH = \frac{(F_1 - MPV)}{MPV} x100$$

where F_1 is the mean performance of the cross and MPV is mean value of the two inbred parents over locations. High parent heterosis was calculated as:

$$HPH = \frac{(F_1 - HPV)}{HPV} x100$$

where HPV is the mean value of the high performing parent. Standard heterosis was calculated against the QPM check hybridized in the study (BHQP542) as:

$$SH = \frac{(F_1 - CH)}{CH} x100$$

where CH is the mean value of the standard check. Significance of the heterosis effects were determined by the t-test, using standard errors of the respective heterosis.

Hybrid sum of squares were partitioned into sums of squares due to general combining ability (GCA) of lines and testers, and specific combining ability (SCA) of the cross combinations using a line x tester model described by Singh and Chaudary (1999). The statistical model used for across locations analysis was as follows (Hallauer and Miranda, 1988):

$Y_{ijk}=\mu+g_i+g_j+s_{ij}+l_k+(gl)_{ik}+(gl)_{jk}+(sl)_{ijk}+e_{ijk}$

where Y_{ijk} is the observed performance of the cross between i^{th} line and j^{th} tester in k^{th} location, μ the overall mean, g_i GCA effect of the i^{th} line, g_j GCA effect of the j^{th} tester, S_{ij} SCA effect of the cross between i^{th} line and j^{th} tester, l_k the location effect, $(gl)_{ik}$ the interaction between GCA effect of the i^{th} line and k^{th} location, $(gl)_{jk}$ the interaction between GCA effect of the j^{th} tester and k^{th} location, $(sl)_{ijk}$ the interaction between

SCA effects of the cross and location, and e_{ijk} pooled error for Y_{ijk} observation.

The relative contribution of GCA and SCA effects to the variation among the hybrids were assessed following the method suggested by Kang (1994). The significance of GCA and SCA sources of variation was determined using the corresponding interactions with the environment as error terms. Mean squares for GCA x location and SCA x location interactions were tested against pooled error. The pooled error mean squares were obtained by dividing the sum of error sum of squares from all combined locations with the corresponding sum of error degrees of freedom and number of replications. Significance of GCA and SCA effects were determined by the t-test, using standard errors of GCA and SCA effects, respectively.

Grain yield SCA effects were used to classify the inbred lines into heterotic groups. To belong into a heterotic, the line must have significant ($P < 0.05$) SCA effects with one of the testers and significant ($P < 0.05$) negative SCA effects with the other. An inbred line was grouped with a heterotic tester with which it revealed significantly negative SCA effect. A line that revealed non-significant or zero SCA effects with the testers was not classified into either heterotic group (Vasal et al, 1992; Legesse et al, 2009).

Results

Performances of parental lines

Analysis of variance for each environment revealed significant difference among parental lines for grain yield, agronomic traits and protein quality parameters (data not shown). Location effect on the performances of parental lines was highly significant for most studied traits except for endosperm modification, tryptophan content and quality index (Table 2). Mean squares due to parents were significant for all traits except for thousand kernel weight and endosperm modification. Similarly, parent x location interaction effects were significant for grain yield and most studied traits, but not for endosperm modification, tryptophan and protein content. Grain yield for parental lines ranged from 1.77 to 4.04 t ha^{-1} with a mean of 2.83 t ha^{-1}. Lines L10 (4.04 t ha^{-1}), L15 (3.69 t ha^{-1}), and L9 (3.65 t ha^{-1}), and tester 142-1-eQ (3.74 t ha^{-1}) had higher grain yield (Table 3). Mean days to anthesis was 109 with a range of 103 – 118 days; whereas days to silking ranged from 109 to 123 with a mean of 114 days. Inbred lines L6, L11, and L13, and tester F-7215Q took shorter days for anthesis and silking. Plant height ranged from 130 to 230 cm with a mean of 170 cm, whereas ear height ranged from 62 to 134 cm with a mean of 88 cm. Inbred lines L2 and L13, and tester F-7215Q had shorter plant and ear heights. Mean ears per plant was 1.26 with a range of 0.98 to 1.55. L8, L9 and L16 had higher ears per plant of greater than 1.5 while 142-1-eQ showed higher ears per plant of 1.25 from the testers.

Among all the parental lines, endosperm modification scores (1 - 5 scale) ranged from 1.50 to 3.33 with a mean of 2.44; whereas tryptophan content ranged from 0.56 to 1.07 g kg^{-1} with a mean of 0.74 g kg^{-1}. Most parental lines had acceptable levels of endosperm modification that was close to 2.0. Among the inbred lines, L2 and L13 had the higher tryptophan contents of 0.91 and 1.07 g kg^{-1}, respectively, while 142-1-eQ showed higher tryptophan level (0.71 g kg^{-1}) from the testers. Protein content ranged between 98 and 131 g kg^{-1} with a mean value of 114 g kg^{-1}; whereas quality index showed a mean of 0.65% with a range of 0.49 to 0.87%. Inbred lines L12 (131 g kg^{-1}) and L13 (123 g kg^{-1}) had higher protein content;

Table 4 - Mean squares for grain yield, agronomic and protein quality traitsof QPM hybrids evaluated across three locations in Ethiopia.

Source	DF	GY (t ha^{-1})	TKW (g)	AD (d)	SD (d)	PH (cm)	EH (cm)	EPP (No.)	MODI (1-5)	TRP (g kg^{-1})	PROT (g kg^{-1})	QI (%)
Location (L)	2	1078.5**	289379.4**	10400.3**	5842.5**	43096.2**	24785.3**	11.1**	0.91	0.05	1284.9**	0.02
Replication/L	3	6.38**	942.87	3.43	19.735	1611.52**	171.79	0.05	0.58**	0.16**	203.7	0.11**
Entry (hybrids+checks)	43	8.86***	6393.4**	26.46	32.50*	1215.84**	627.34**	0.08	1.69**	0.09**	360.93**	0.07**
Hybrid (H)	39	8.50**	4978.96**	24.28	31.97*	1074.27**	514.48**	0.081	1.41*	0.08**	331.48**	0.06**
GCALine	19	6.17**	6264.32**	21.28	35.92*	1606.91**	697.43**	0.11	1.17	0.10**	316.30**	0.08**
GCA Tester	1	91.76**	167.50	262.50**	148.84**	20.42	1606.84*	0.22	0.34	0.01	2048.29**	0.15*
SCA	19	6.45**	3946.84*	14.75	21.86	597.10**	274.05	0.04	1.71*	0.07**	261.41**	0.04*
L*Entry	86	2.20**	3398.97**	23.16	25.90	250.23	279.35**	0.06	1.17	0.02	123.05	0.02
L*Hybrid	78	2.04*	3590.96**	23.36	26.21	239.94	261.07	0.06	1.28*	0.02	128.41	0.02
L*GCALine	38	2.06*	3667.07*	33.28*	38.14**	245.67	247.25	0.05	0.96	0.02	158.44*	0.02
L*GCATester	2	3.18	22157.62**	1.82	11.45	262.00	105.35	0.08	3.46*	0.00	29.28	0.01
L*SCA	38	1.96	2537.66	14.58	15.07	233.04	283.09	0.08	1.48*	0.02	105.8	0.02
Error	129	1.28	2042.02	21.18	19.66	208.93	256.57	0.09	0.86	0.02	99.10	0.02
%SS GCA		63.04	61.38	70.41	66.68	72.92	74.05	75.24	40.99	58.95	61.87	68.72
%SS SCA		36.96	38.62	29.59	33.32	27.08	25.95	24.76	59.01	41.05	38.13	31.28
Mean		7.61	300.54	104.39	107.93	256.49	143.50	1.42	2.14	0.73	103.50	0.71
Minimum		5.62	212.70	100.00	102.17	219.50	118.67	1.17	1.17	0.53	86.17	0.48
Maximum		10.40	375.93	109.50	113.00	282.33	167.00	1.82	3.50	0.99	120.17	0.91
CV (%)		14.88	15.04	4.41	4.11	5.64	11.16	20.64	43.30	20.46	9.62	20.08
SE(M)±		0.46	18.45	1.88	1.81	5.90	6.54	0.12	0.38	0.06	4.06	0.06

* P< 0.05, ** P< 0.01, DA = days to anthesis, DF = degrees of freedom, DS = days to silking, EH = ear height, EPP = ears per plant, GY= Grain yield, MODI = Endosperm modification, PH = Plant height, PROT = Protein content, QI = Quality index, TKW = Thousand kernel weight, TRP = tryptophan content.

Table 5 - Mean grain yield, agronomic and protein quality traits of top-yielding 10 QPM hybrids and standard checks evaluated across three locations in Ethiopia.

Cross	Grain yield (t ha^{-1})				TKW	DS	PH	EH	EPP	MODI	TRP	PROT	QI
	Ambo	Holeta	Kulumsa	Across	(g)	(d)	(cm)	(cm)	(No.)	(1-5)	(g kg^{-1})	(g kg^{-1})	(%)
L20 x 142-1-eQ	6.20	11.05	13.95	10.40	308	109	270	147	1.45	2.17	0.66	95	0.69
L17 x 142-1-eQ	6.65	10.65	12.95	10.08	302	108	282	167	1.47	1.83	0.77	107	0.73
L19 x 142-1-eQ	5.45	9.85	14.10	9.80	269	110	267	164	1.32	1.33	0.70	108	0.66
L12 x 142-1-eQ	4.00	9.20	15.75	9.65	262	106	265	147	1.47	1.83	0.97	117	0.83
L16 x 142-1-eQ	5.25	9.60	14.05	9.63	317	110	254	139	1.33	2.67	0.76	101	0.75
L15 x 142-1-eQ	4.75	10.40	13.00	9.38	333	110	269	149	1.42	1.50	0.62	98	0.63
L5 x 142-1-eQ	4.40	9.10	13.55	9.02	257	108	263	155	1.45	1.67	0.57	91	0.64
L10 x 142-1-eQ	4.15	10.55	12.20	8.97	291	111	278	162	1.27	1.83	0.67	99	0.69
L3 x 142-1-eQ	4.35	8.85	12.25	8.48	347	111	268	150	1.25	1.83	0.69	109	0.64
L9 x 142-1-eQ	4.70	7.90	12.50	8.37	321	110	265	150	1.38	1.83	0.55	90	0.62
Mean	3.96	7.94	10.94	7.61	301	108	256	144	1.42	2.14	0.73	104	0.71
LSD	2.27	2.34	2.25	1.29	51.62	5.06	16.51	18.3	0.33	1.06	0.17	11.37	0.17
Checks													
MH800	4.35	6.70	11.05	7.37	334	107	235	139	1.42	1.33	0.57	120	0.48
BH660	6.10	8.70	14.25	9.68	368	113	279	166	1.55	1.33	0.53	91	0.58
BHQP542	2.60	6.05	8.30	5.65	213	106	231	119	1.48	1.17	0.78	104	0.75
BH540	6.30	6.60	9.80	7.57	301	108	247	142	1.45	1.5	0.53	103	0.51

DF = Degrees of freedom, DS = Days to silking, EH = Ear height, EPP = Ears per plant, MODI = Endosperm modification, PH = Plant height, PROT = Protein content; QI: Quality index, TKW = Thousand kernel weight; TRP = Tryptophan content.

whereas L13 (0.87%) and L18 (0.80%) had higher protein quality index. From the testers, F-7215Q had higer protein content (112 g kg^{-1}) while 142-1-eQ had higher quality index of 0.71%.

Hybrid performances

At each location, significant differences were observed among the hybrids for grain yield, agronomic and protein quality traits (data not shown). Combined analysis of variance showed that mean squares attributed to location were highly significant for most traits except for endosperm modification, tryptophan content and quality index (Table 4). Significant entry (hybrids + checks) and hybrid mean squares were observed for grain yield and other traits except for days to anthesis and ears per plant. Entry x location interaction effect was highly significant for grain yield, thousand kernel weight and ear height, whereas hybrid x location effect was significant for grain yield, thousand kernel weight and endosperm modification. Across locations, mean grain yield of the hybrids ranged from 5.62 t ha^{-1} to 10.40 t ha^{-1} with a mean of 7.62 t ha^{-1}. Many QPM hybrids showed higher grain yield than the standard checks (Table 5). Test crosses L20 x 142-1-eQ (10.4 t ha^{-1}), L17 x 142-1-eQ (10.1 t ha^{-1}) and L19 x 142-1-eQ (9.80 t ha^{-1}) showed higher grain yield than the best non-QPM check, BH660 (9.68 t ha^{-1}) and the QPM check, BHQP542 (5.65 t ha^{-1}). As indicated in Table 5, all the 10 top-yielding testcross hybrids contained tester 142-1-eQ as one of the parents. Thousand kernel weight ranged from 213 to 376 g with a mean of 301 g. Most top-yielding QPM hybrids had higher kernel weight than the overall mean, but lower than the best non-QPM check, BH660 (368 g). Days to silking ranged from 102 to 113 days, with a mean of 108 days. Days to silking for almost all the 10 top-yielding hybrids were the same as or higher than the overall mean, except for L12 x 142-1-eQ. The highest yielding standard check hybrid, BH660, was the latest to silk (113 days). Plant height ranged between 220 cm and 282 cm, with a mean of 257 cm; whereas ear height ranged from 119 to 167 cm, with a mean of 144 cm. Most of the top-yielding hybrids had taller plant and ear heights than the grand mean, except L16 x 142-1-eQ. BH660, the highest yielding check, had taller plant (279 cm) and ear (166 cm) height than most of the QPM hybrids.

Endosperm modification ranged from 1.17 to 3.50, with a mean of 2.14; whereas tryptophan content ranged between 0.53 and 0.99, with a mean of 0.73. Most top-yielding hybrids showed endosperm modification score (1 – 5 scale) of less than 2.0, except L20 x 142-1-eQ and L16 x 142-1-eQ. Some of the top-yielding hybrids had higher tryptophan content than the overall mean, whereas only L12 x 142-1-eQ had higher tryptophan level (0.97 g kg^{-1}) than the QPM check, BHQP542 (0.78 g kg^{-1}). Protein content ranged from 86.2 to 120.2 g kg^{-1}, with a mean of 103.5 g kg^{-1}; whereas quality index ranged between 0.48 and 0.91%, with a mean of 0.71%. Crosses L17 x 142-1-eQ, L12 x 142-1-eQ and L16 x 142-1-eQ had higher or similar levels of protein content and protein quality index as compared to the overall mean and the QPM check.

Estimates of heterosis

Among all the tested traits, grain yield had the highest mid parent and better parent heterosis while endosperm modification and thousand kernel weight had higher standard heterosis (Table 6). All the crosses showed positive and high mid parent and high parent heterosis for grain yield. Mid parent heterosis for grain yield ranged between 81.2 and 315.9%, with mean of 180.2%; whereas high parent heterosis ranged from 61.0 to 281.8% with a mean of 138.4%. Crosses L1 x F7215Q, L13 x F7215Q, and L14 x F7215Q showed higher (above 200%) mid parent and high parent heterosis for grain yield. More than 85% of the QPM crosses showed positive and high mid-parent and better-parent heterosis for thousand kernel weight. For days to silking, almost all the crosses showed desirable mid-parent and better-parent het-

Table 6 - Mean grain yield, agronomic and protein quality traits of top-yielding 10 QPM hybrids and standard checks evaluated across three locations in Ethiopia.

	Mid Parent Heterosis					High parent heterosis					Standard heterosis				
	Mean	Min	Max	Superior crosses (%)	LSD	Mean	Min	Max	Superior crosses (%)	LSD	Mean	Min	Max	Superior crosses(%)	LSD
GY (t ha^{-1})	180.2	81.2	315.9	100	1.585	138.4	61.0	281.8	100	1.29	34.9	-0.5	84.1	97.5	1.29
TKW (g)	16.2	-2.9	40.3	92.5	63.22	10.5	-6.5	39.9	85	51.62	41.1	19.0	76.7	100	51.62
DS (d)	-6.9	-12.0	-1.9	100	6.203	-4.4	-13.1	2.7	95	5.06	1.5	-3.9	6.3	27.5	5.06
PH (cm)	41.8	13.4	68.6	0	20.22	58.8	35.0	89.9	0	16.51	11.2	-5.1	22.0	5	16.51
EH (cm)	41.2	18.1	72.4	0	22.41	72.8	37.1	148.3	0	18.30	21.1	6.9	40.7	0	18.30
MODI (1-5)	-3.0	-46.8	45.6	65	1.296	7.6	-38.6	78.0	37.5	1.06	89.8	13.7	199.1	0	1.06
TRP (g kg^{-1})	6.2	-21.4	43.0	57.5	0.208	-2.5	-33.8	40.6	40	0.17	-5.0	-29.5	26.9	30	0.17
PROT (g kg^{-1})	-5.7	-17.7	1.4	15	13.93	-10.1	-25.3	-3.0	0	11.37	-0.6	-17.1	13.8	52.5	11.37
QI (%)	13.0	-15.2	51.1	65	0.198	3.8	-25.5	41.7	52.5	0.16	-4.0	-29.8	21.3	35	0.16

DF = Degrees of freedom, DS = Days to silking, EH = Ear height, MODI = Endosperm modification, PH = Plant height, PROT = Protein content, QI = Quality index, TKW = Thousand kernel weight, TRP = Tryptophan content.

erosis. Only few or none of the crosses had desirable mid parent and better parent heterosis for plant and ear height, and protein content. Considerable proportion of the QPM crosses showed higher mid parent heterosis for endosperm modification (65%), tryptophan content (58%), and protein quality index (65%). Less than 50% of the QPM crosses showed desirable better parent heterosis for endosperm modification (38%) and tryptophan content (40%); whereas about 53% of the crosses showed superior protein quality index over the better parent.

The highest standard heterosis was observed for endosperm modification with a mean value of 89.8%, and range of 13.7 to 199.1%. For grain yield, it ranged from –0.5 to 97.5% with a mean value of 34.9%. The highest standard heterosis was observed for the top yielding crosses (Table 5), L17 x 142-1-eQ (78.4%), L19 x 142-1-eQ (73.5%), and L20 x 142-1-eQ (84.1%). Almost all the QPM crosses had higher grain yield and thousand kernel weight than the standard QPM check hybrid as depicted by positive standard heterosis of the crosses. Many crosses showed desirable heterosis for protein content (53%); whereas only few or none of the crosses showed acceptable standard heterosis for days to silking (28%), plant (5%) and ear height (0%), endosperm modification (0%), tryptophan content (30%) and quality index (35%).

Combining ability estimates

Line by tester analysis indicated that mean squares attributable to line GCA were significant for most traits except for days to anthesis, ears per plant and endosperm modification (Table 4). Tester GCA effects were significant for grain yield, days to anthesis and silking, ear height, protein content and quality index. Mean squares attributable to SCA were significant for most traits, but not for days to anthesis and silking, ear height and ears per plant. The contributions of GCA sum of squares (i.e., GCA_{lines} plus GCA-testers) to the variation among the hybrids were larger than SCA sum of squares for most traits, except for endosperm modification which showed larger SCA sum of square (59%) than the GCA sum of square (41%). All other traits such as grain yield (63%), thousand kernel weight (61%), days to anthesis (70%) and silking (67%), plant height (73%), ear height (74%), number of ears per plant (75%), tryptophan content (59%), protein content (62%) and quality index (69%) had larger GCA sum of squares than that of SCA. The contributions of GCA_{lines} were much larger than $GC_{testers}$ for all traits. Location x GCA_{lines} interaction effects were significant for grain yield, thousand kernel weight, days to anthesis and silking and protein content. Location x $GCA_{testers}$ was significant only for thousand kernel weight and endosperm modification, whereas location x SCA mean square was significant only for endosperm modification.

A wide range of variability was observed for GCA effects among the 20 inbred lines and between the two testers for all traits. For grain yield, for example, line GCA effects ranged from -1.29 (L6) to 1.01 (L17) t ha^{-1} (Table 7); whereas tester GCA effects were 0.62 t ha^{-1} for 142-1-eQ and -0.62 for F7215Q. Inbred lines L12, L17, L19, and L20 had positive and significant GCA effects, whereas inbred lines L2, L6, L11, and L18 had highly significant negative GCA effects for grain yield. Inbred lines L8 and L14 had highly significant positive GCA effects, whereas L6 had significantly negative GCA effects for thousand kernel weight. L6 showed highly significant GCA effects, whereas L2 had positive and significant GCA effects for silking date. For plant and ear height, inbreds L2 and L4 showed desirable GCA effects. In terms of protein quality traits, L12 and L13 were found to be good combiners for both protein quantity and quality, whereas inbred lines L4, L5, L7, and L15 were poor combiners for protein quality. From the testers, F7215Q showed highly significant negative GCA effects for days to anthesis (-1.05 days) and silking (-0.79 days), and ear height (-2.59 cm); and highly significant positive GCA effects for protein content (2.82 g kg^{-1}) and quality index (0.03%). Tester 142-1-eQ showed positive and highly significant GCA effect (0.01 g kg^{-1}) for tryptophan content.

Variable SCA effects were observed among the QPM crosses for most of the studied traits. Eight hybrids involving each tester showed significant and positive SCA effects for grain yield. Among these, L6 x F7215Q (0.94 t ha^{-1}), L16 x 142-1-eQ (0.95 t ha^{-1}), L18 x F7215Q (0.98 t ha^{-1}), and L20 x 142-1-eQ (1.42

t ha^{-1}) had higher SCA effects. Hybrids L2 x F7215Q and L3 x 142-1-eQ had significantly positive SCA effects for thousand kernel weight (data not shown). For plant height, L8 x 142-1-eQ, L9 x F7215Q, and L18 x 142-1-eQ showed significantly low SCA effects, whereas L13 x F7215Q had the lowest SCA for endosperm modification. Crosses L2 x 142-1-eQ, L3 x F7215Q and L10 x F7215Q showed positive and significant SCA effects for tryptophan content and quality index, whereas L5 x F7215Q and L17 x 142-1-eQ had the highest positive SCA effects for protein content.

The two testers used in the current study showed highly contrasting GCA effects for grain yield and other traits, and could safely be used to assign the inbred lines into heterotic groups. Lines that had positive SCA effects with 142-1-eQ and negative SCA effects with A7215Q were include under Heterotic Group A. Conversely, lines that had positive SCA effects with A7215Q and negative SCA effects with 142-1-eQ were grouped under Heterotic Group B. Accordingly, eight inbred lines were categorized under each heterotic group (Table 7). Four of the inbred lines that revealed non-significant SCA effects with the testers were not classified into either heterotic group.

Discussion

Significant differences observed among the parental lines and hybrids for grain yield, agronomic and protein quality traits showed the existence of variations among the genotypes studied, which allows the selection of preferred inbred lines and hybrids. Variations among QPM genotypes for these traits have previously been reported by several investigators (Machida et al, 2010; Pixley and Bjarnason, 1993; Wegary et al, 2011; 2014). Location effects were significant for grain yield and yield components, but not significant for endosperm modification, tryptophan content and quality index. Contrary to this finding, several researchers previously reported significant location effect on endosperm modification, tryptophan content and quality index (Pixley and Bjarnasan, 2002; Machida et al, 2010; Wegary et al, 2011). The contrasts in these findings could be explained by the differences in germplasm and test locations used.

Significant interactions of hybrids and inbred lines with locations for grain yield and some agronomic traits indicated that the performance of these genotypes were not consistent across locations. Similar to the current finding, the existence of G x E interaction in QPM hybrids was reported by many other investigators (Vasal et al, 1993; Pixley and Bjarnason, 1993; 2002; Musila et al, 2010). In most cases, inbred line x

Table 7 - GCA effects of QPM inbred lines for grain yield, agronomic and protein quality traits evaluated across three locations in Ethiopia.

	General combining ability (GCA)								GY SCA		Heterotic
Line	GY	TKW	SD	PH	EH	TRP	PRT	QI	142-1-eQ	F7215Q	group
L1	0.31	5.16	-1.72	-5.98	-3.65	0.06	-2.33	0.08	-0.79**	0.79**	B
L2	-0.99**	13.29	2.70*	-20.98**	-8.81	0.07	-0.25	0.07	0.40**	-0.40**	A
L3	0.16	10.61	1.86	9.85*	0.77	0.04	3.84	0.02	0.08	-0.08	-
L4	-0.74*	-21.09	1.86	-29.15**	-13.98**	-0.11*	5.75*	-0.14**	-0.70**	0.70**	B
L5	0.66*	-31.42*	0.28	2.43	6.27	-0.09*	1.34	-0.09*	0.12	-0.12	-
L6	-1.29**	-27.82*	-3.89**	-1.40	-8.56	0.01	-9.83**	0.10**	-0.94*	0.94*	B
L7	-0.40	-17.92	1.20	0.10	8.69	-0.12**	0.59	-0.12**	0.08	-0.08	-
L8	-0.13	54.16**	-2.22	-0.57	-0.06	-0.02	-7.66**	0.03	-0.41**	0.41**	B
L9	-0.01	11.95	-0.47	-2.98	-0.06	-0.12**	-6.16*	-0.08	0.14	-0.14	-
L10	0.42	-13.65	1.28	12.10**	7.10	0.06	-0.14	0.05	0.31**	-0.31**	A
L11	-0.98**	-5.03	-1.22	10.02*	1.10	0.06	-3.25	0.09*	-0.89**	0.89**	B
L12	0.93**	-27.94*	-1.14	2.35	4.69	0.13**	11.84**	0.03	0.48**	-0.48**	A
L13	-0.09	11.21	-1.05	-7.65	-8.48	0.21**	7.50**	0.14**	-0.66**	0.66**	B
L14	-0.49	35.10**	-1.97	-7.98	-4.48	0.03	-1.33	0.03	-0.84**	0.84**	B
L15	0.33	15.08	0.11	13.35**	5.44	-0.10**	1.25	-0.11**	0.82**	-0.82**	A
L16	0.45	-1.40	1.86	-7.57	-8.56	0.06	2.59	0.03	0.95**	-0.95**	A
L17	1.01**	-3.15	1.20	15.68**	15.69**	-0.07	-0.58	-0.05	0.84**	-0.84**	A
L18	-0.88**	-25.68	-0.64	-3.23	-2.56	0.01	-2.91	0.03	-0.98**	0.98**	B
L19	0.99**	-7.74	1.78	9.35*	10.35*	-0.04	3.34	-0.06	0.57**	-0.57**	A
L20	0.74*	26.29	0.20	12.27**	-0.90	-0.07	-3.58	-0.04	1.42**	-1.42**	A
SE(gi)	0.33	13.31	1.29	4.41	4.46	0.05	2.87	0.04	0.11		

* P< 0.05, ** P< 0.01, DF = Degrees of freedom, DS = Days to silking, EH = Ear height, GY = Grain yield, MODI = Endosperm modification, PH = Plant height, PROT = Protein content, QI = Quality index, SE(gi) = Standard error of the GCA, TKW = Thousand kernel weight, TRP = Tryptophan content.

location and hybrid x location interaction effects were not significant for endosperm modification and protein quality traits indicating consistent performance of the studied genotypes for these traits. It also depicted that the ranking of genotypes for these traits were similar across the test locations, which would enable selection for stable endosperm modification and protein quality traits. Previously similar findings were reported for endosperm modification (Pixley and Bjarnason, 1993), and for tryptophan content and quality index (Machida et al, 2010).

Many of the inbred lines used in the current study showed acceptable grain yield, agronomic performances, endosperm modification and protein quality traits (Table 2). According to Vivek et al (2008) a QPM genotype should have endosperm modification score close 2.0, minimum levels of 0.80% quality index, 0.75 g kg^{-1} tryptophan and 80 g kg^{-1} protein in whole grain. In addition to grain yield and agronomic performances, inbred lines that showed desirable levels of endosperm modification and protein quality traits could be used as sources of gene in the highland QPM breeding program and for QPM variety development. Most of the 10 top-yielding QPM hybrids fulfilled the required standards for endosperm modification and protein content; but only few hybrids did exceed the established threshold values for tryptophan content and quality index (Table 5). Thus appropriate breeding strategies should be designed to develop QPM hybrids with acceptable quality standards. On the other hand, all the QPM hybrids consistently showed higher tryptophan content and quality index than the non-QPM check hybrids, indicating the superiority of QPM genotypes for protein quality as previously reported (Vasal, 2001).

The existence of high positive mid-parent and better-parent heterosis for grain yield indicated the presence of substantial heterosis in the studied hybrids. Among all the traits studied, mid parent and better parent heterosis were the highest for grain yield, which is in line with the findings of Wegary et al (2013). The level of mean mid parent (180.2%) and better-parent (138.4%) heterosis observed for grain yield in the present study is higher than that reported by Wegary et al (2013), but lower than that reported by Saleh et al (2002). The hybrids had heavier thousand kernel weight than the parental lines as depicted by positive mid-parent and better-parent heterosis. For days to silking, most hybrids showed desirable negative heterosis, indicating that the hybrids were earlier in silking than their parental lines. High positive mid-parent and better-parent heterosis for ear and plant height indicated the preponderance of dominance effects among parental lines for taller plant stature. These results are in agreement Wegary et al (2013), who observed taller plant stature in hybrid progenies as compared to the parental inbred lines. The existence of heterosis in QPM hybrids for endosperm modification, tryptophan content and quality index is desirable for exploitation of heterosis to increase levels of these traits in the breeding program. On the other hand, the absence of heterosis for protein content is regrettable as this effect cannot be exploited to directly contribute to the gains for the trait.

Desirable standard heterosis depicted by the QPM crosses for grain yield, most agronomic and protein quality traits indicated that the hybrids had added advantage of being superior to the QPM check hybrid for these traits. Hybrids that combine desirable traits can be used as important source materials in the highland QPM breeding program. Almost all the QPM hybrids showed high positive standard heterosis for plant stature and endosperm modification indicating that the hybrids were taller and had more opaque kernel phenotypes than the QPM check hybrid.

The significant GCA and SCA mean squares for grain yield and some agronomic traits indicated that the variability observed among the hybrids was attributed to additive and non-additive gene effects. This finding is in agreement with the reports of previous studies conducted on the combining ability of QPM inbred lines (Pixley and Bjarnason, 1993; Wegary et al, 2014). Only the GCA effects were significant for days to silking and ear height, depicting the importance of additive gene effects. On the other hand, non-additive gene effects were significant in the inheritance of endosperm modification. Contrary to the current finding, Pixley and Bjarnasan (1993) and Vasal et al (1993) reported that additive gene effects are more important than non-additive effects for endosperm modification in QPM.

According to Kang (1994), the ratio of GCA and SCA sum of squares are used in comparing the relative importance of these effects in a fixed model. In this study, GCA effects (mainly GCA of lines) accounted for most of the variations among the hybrids for most studied traits, suggesting that the traits were conditioned mainly by genes with additive effects. Grain yield and some agronomic traits showed significant GCA x location interaction, indicating that GCA effects for these traits were not consistent across locations. Similarly, Vasal et al (1993), Wegary et al (2014) and Musila et al (2010) reported significant GCA x location interaction in QPM inbred lines for grain yield and agronomic traits. SCA effects of almost all traits were consistent across locations as evident from non-significant SCA x location interactions. Similar finding were reported by Musila et al (2010) for diallel crosses of QPM inbred lines evaluated across locations. The absence of significant interaction of GCA and SCA effects with locations for tryptophan content and quality index, indicated the consistence of these effects across locations and hence, possible to select lines and crosses with desirable combining ability effects for these quality traits.

The estimate of GCA effects of a parental line is an important indicator of its potential for generating

superior breeding genotypes. Hallauer and Miranda (1988) stated that inbred lines that have superior GCA are retained for further use in the breeding program. In this study, a wide range of GCA effects were observed (Table 7), indicated the presence of diversity in the genetic constitution of the QPM inbred lines for measured traits. Inbred lines L5, L12, L17, L19, and L20 were good general combiners for grain yield, indicating that these lines contributed to higher grain yield in their crosses. On the contrary, L2, L6, L11, and L18 were poor general combiners for grain yield, indicating that these lines were not desirable for the development of high yielding hybrids. L8 and L14 were found to be the best general combiners for thousand seed weight. L6 is the only inbred line which showed desirable GCA effects for days to silking. This inbred line, however, was poor general combiner for grain yield. As stated by Pswarayi and Vivek (2008), earlier maturing genotype, owing to its shorter life cycle, is predisposed to lower yields than a later maturing genotype which has the opportunity to draw nutrients and photosynthesize over a longer period. For ear and plant height, inbred lines L2 and L4 had desirable GCA effects, whereas the GCA effects of L10, L15, L17, L19, and L20 were undesirable as taller plants are more prone to lodging. Inbred lines L12 and L13 were the best general combiners for tryptophan and protein content, and quality index and can be used in QPM variety development and pedigree breeding program as these inbred lines contributed to improved levels of protein quantity and quality. In terms of testers, 142-1-eQ was good general combiner for grain yield and tryptophan content, whereas F7215Q was found to be desirable for anthesis and silking date, ear height, protein content and quality index.

Significant SCA effects indicated that the crosses performed better or poorer than what would be expected based on GCA effects of the respective parents. This is evident from the fact that some of the crosses, L6 x F7215Q and L18 x F7215Q, with the highest SCA effects for grain yield involved inbred lines and a tester with significantly low GCA effects. High SCA value indicates the significance of non-additive gene action and thus it is manifested between crosses of two genetically divergent parental lines, mainly due to the preponderance of dominant gene effects. Significantly variable SCA effects observed among the QPM crosses for most studied traits implied that selection based on SCA effects could be used to pick good hybrids.

Among other factors, SCA effects are used as important criteria for identification of heterotic groups among maize genotypes (Legesse et al, 2009; Pswarayi and Vivek, 2008; Vasal et al, 1992). Positive SCA effects for grain yield indicate that lines are in opposite heterotic groups while negative SCA effects indicate that lines are in the same heterotic group (Pswarayi and Vivek, 2008; Vasal et al, 1992). Most of the inbred lines used in the current study were distinctive with respect to their heterotic patterns as observed from the significantly positive or negative SCA effects for grain yield. However, as combining abilities are specific to the group of parents being tested, changes might be expected in the heterotic behavior observed in the current study. Rawlings and Thompson (1962) stated that lines belonging to the same heterotic group may not have absolutely identical heterotic patterns because of small differences in the alleles they may be carrying. Similarly, in this study, lines that were derived from the same genetic background were not necessary assigned to the same heterotic group.

Heterotic groups A and B at CIMMYT have been aligned similar to some of the well-known heterotic patterns across the globe; viz. Tuxpeño vs. ETO Blanco of Mexico, Reid Yellow Dent vs Lancaster of the USA, Kitale vs. Ecuador of the east African highlands and N3 vs SC of southern Africa. Thus, group A is thought to exhibit heterosis similar to Kitale,Tuxpeño, N3, and Reid. Group B is thought to exhibit heterosis similar to Ecuador, ETO, SC, Blanco, and Lancaster (Pswarayi and Vivek, 2008). In the highland QPM breeding program,heterosis can be exploited by crossing the lines from different heterotic groups. For a breeding program geared towards development of three-way hybrids, this presents better opportunity where hybrids could be developed using the two heterotic groups (e.g. A x A single cross crossed to a line from group B). Tropical maize germplasm is known to have an intra-group diversity (Pswarayi and Vivek, 2008) that is sufficient to exploit the heterosis for seed production in three-way and double cross combinations. Higher yielding single cross can be developed from higher-yielding as well as good combining inbred lines that belongs to the same heterotic group by largely exploiting additive variance while retaining the dominance effects to be fully exploited in the final across heterotic group of three-way cross hybrid.

Conclusion

The study indicated the existence of high level of variability among the inbred lines and hybrids, and the possibility of improving QPM germplasm for the traits evaluated. The desirable heterosis observed for grain yield, agronomic and protein quality traits indicated the potential of the inbred lines for hybrid development. GCA effects were primarily responsible for variation of most traits studied, indicating the preponderance of additive gene effects. Inbred lines and hybrids with desirable combining ability effects for traits of interest can be effectively used in QPM variety development program. In addition, heterosis can be exploited through systematic hybridization of desirable parents based on the heterotic patterns observed in the set of materials used in the current study.

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